Saupe, E., Farnsworth, A., Lunt, D., Sagoo, N., Pham, K., & Field, D. (2019). Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(26), 12895-12900. https://doi.org/10.1073/pnas.1903866116

Classification: Biological Sciences: Evolution

Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic

Erin E. Saupe[a,1,*], Alexander Farnsworth[b], Daniel J. Lunt[b], Navjit Sagoo[c], Karen V. Pham[d], Daniel J. Field[e,1,*]

*These authors contributed equally

[a] Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, OX1 3AN, UK

[b] School of Geographical Sciences, University of Bristol, University Road, Clifton, Bristol BS8 1SS, UK

[c] Department of Meteorology, Stockholm University, 106 91 Stockholm, Stockholm, Sweden

[d] Division of Geological and Planetary Sciences, Caltech, Pasadena, California, USA, 91125

[e] Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK

[1]To whom correspondence should be addressed: erin.saupe@earth.ox.ac.uk; djf70@cam.ac.uk

Many higher-level avian clades are restricted to Earth's lower latitudes, leading to historical biogeographic reconstructions favoring a Gondwanan origin of crown birds and numerous deep subclades. However, several such 'tropical-restricted' clades are represented by stem-lineage fossils well outside the ranges of their closest living relatives, often on northern continents. To assess the drivers of these geographic disjunctions, we combine ecological niche modeling, paleoclimate models, and the early Cenozoic fossil record to examine the influence of climatic change on avian geographic distributions over the last ~56 million years. By modeling the distribution of suitable habitable area through time, we illustrate that most Paleogene fossil-bearing localities would have been suitable for occupancy by extant clade representatives when their stem-lineage fossils were deposited. Potentially-suitable habitat for numerous higher-level clades is inferred to have become progressively restricted towards the tropics throughout the Cenozoic, culminating in relatively narrow circumtropical distributions in the present day. Our results are consistent with coarse-scale niche conservatism at the clade level, and support a scenario whereby climate change over geological timescales has largely dictated the geographic distributions of major avian clades. The distinctive modern bias towards high avian diversity at tropical latitudes for most hierarchical taxonomic levels may therefore represent a relatively recent phenomenon, overprinting a complex biogeographic history characterized by dramatic geographic range shifts driven by Earth's changing climate, variable persistence, and intercontinental dispersal. Earth's current climatic trajectory portends a return to a megathermal state, which may dramatically influence the geographic distributions of many range-restricted extant clades.

Keywords: Climate change, niche conservatism, latitudinal diversity gradient, ecological niche modeling, Paleogene, historical biogeography

Significance Statement.

The fossil record reveals evidence of dramatic distributional shifts through time for many groups of organisms. One striking example is the early fossil record of modern birds, which shows that many bird groups currently restricted to the tropics were formerly found at high latitudes in North America and Europe. Tracking potentially-suitable habitat for these clades over the last 56 million years reveals that cooling trends throughout this period largely dictated the geographic distributions of these 'tropical' groups, complicating our understanding of where on Earth many of these lineages originated.

Extant avian biodiversity is represented by nearly 11,000 living species, which inhabit virtually every conceivable subaerial environment from the poles to the equator (1). However, despite the ubiquity of birds and their penchant for dispersal, extant birdlife is unequally distributed across the Earth. In particular, avian diversity—in terms of both species numbers and higher taxonomic groups—is skewed towards tropical environments on the southern continents (i.e. those that formerly composed the Mesozoic supercontinent of Gondwana).

This pattern led earlier avian historical biogeographic investigations to conclude that vicariance driven by Gondwanan breakup, which was largely completed by the end of the Mesozoic, played a predominant role in triggering deep phylogenetic and geographic divergences within crown birds (e.g. (2)). However, recent phylogenetic divergence time studies suggest that most deep divergences within crown birds took place after the K-Pg mass extinction (3-7), roughly 66.02 million years ago (8). Although Australia, Antarctica, and South America maintained connectivity into the Paleogene (9, 10), Mesozoic Gondwanan vicariance appears to have played no role in either the diversification or geographic expansion of the avian crown group. Nonetheless, analytical reconstructions of higher-order avian historical biogeography invariably recover strong evidence for an origin of most modern diversity on southern landmasses (2, 6, 11).

The crown bird fossil record has unique potential to reveal where different groups of birds were formerly distributed in deep time. Fossil evidence, for example, has long indicated that total-group representatives of clades restricted to relatively narrow geographic regions today were formerly found in different parts of the world (12-21). In particular, the Paleogene record of fossil birds has yielded abundant evidence that many extant clades restricted to southern landmasses had fossil stem-group representatives in the Northern Hemisphere (e.g., 11-13, 15,

19, 21-35). Collectively, such biogeographic disjunctions between early stem group representatives and extant taxa cloud our ability to infer ancestral ranges for the deepest crown bird subclades. The general sparseness and Northern Hemisphere bias of the avian fossil record, however, has limited attempts to incorporate bird fossils into large-scale hypotheses of avian biogeographic evolution. Even studies that have integrated phylogenetically-constrained avian fossils into analytical reconstructions of ancestral biogeography (6) have been criticized for effectively 'swamping out' information from the fossil record by virtue of the limited amount of fossil data compared to extant data in such analyses (36). Thus, ancestral biogeographic reconstructions may have limited potential to reveal whether modern geographic distributions of avian higher clades are truly reflective of their areas of origin, or instead obscure a history of profound biogeographic shifts throughout their evolutionary history.

The avian fossil record reveals information on where early representatives of various lineages were found, and, just as importantly, when in Earth history these birds lived. Paleontological evidence for major fluctuations in avian historical biogeography therefore raises questions about the extent to which historical factors, such as Cenozoic climatic change, may have been responsible for driving historical shifts in avian geographic range, as has been demonstrated for ectothermic clades such as turtles (37) and dismissed as a factor influencing the demise of non-avian dinosaurs in the Late Cretaceous (38). Here, we integrate both past and present avian distributional data and climate characterizations to model how habitable regions for 10 neornithine higher-level clades (Fig. 1) have changed throughout the Cenozoic. We test whether we can predict the presence of high-latitude Paleogene fossil occurrences of these 10 clades, which are currently restricted to tropical and subtropical latitudes, given climatic niche conservatism and estimates of paleoclimate. On the basis of our analyses, we suggest that

climatic changes have played a major role in forcing range contractions for all of these major 'tropical' clades towards their present-day geographic distributions. Our results have important implications for the study of avian historical biogeography in deep time, and that of other vagile, climatically-sensitive clades.

Results

We modeled suitable habitat for 10 neornithine higher-level clades using Maxent (39). The number of environmentally unique occurrences used in model calibration ranged from 103 (Leptosomidae) to 9545 (Trogonidae; Table S1). Model verification exercises suggest that Maxent models of clade tolerances were statistically significant (p-value < 0.05; Table S1). Discriminatory capacity of the model was evaluated using AUC scores; all scores were high and ranged from 0.73 (Trogonidae) to 0.97 (Leptosomidae and Steatornithidae; Table S1).

Suitable conditions were modeled for each clade in the present; these models were then transferred (projected) onto estimates of past climate for four Paleogene time periods with avian fossil records: Ypresian (~56–47.8 Ma), Priabonian (~38–33.9 Ma), Rupelian (~33.9–28.1 Ma) and Chattian (~28.1–23.03 Ma) (Figs. S1–20). We then evaluated whether these paleo-projections correctly predicted penecontemporaneous fossil occurrences for each total clade (Fig. 2 and Figs. S21–30). Of 19 Paleogene clade/locality occurrences investigated, only four were not predicted as highly suitable by our ecological models (Table 1; Fig. 2 & Figs. S21–30). Virtually all Ypresian-aged fossil localities were predicted as suitable, but more recent (Priabonian–Chattian) fossil occurrences were predicted with less fidelity (Table 1). Even so, all younger fossil occurrences aside from one (Todidae) were predicted as suitable under at least one paleo-plate and threshold model, and when suitable habitat was not predicted by our ecological models,

it was usually (~60%) found within only 150 km of a clade-specific Paleogene fossil locality—potentially within levels of paleo-plate reconstruction uncertainty (Table 1).

Our ability to predict fossil occurrences was not dependent on the geographic extent of estimated suitable habitat for a given time slice and clade. That is, predicted suitable habitat ranged from only 3.75% (Todidae, MaxSSS threshold) to 23.61% (Podargidae, LTP threshold) of terrestrial areas globally in fossil-bearing time periods (Table 1). Moreover, present-day models did not predict suitable habitat at the modern position of fossil localities, aside for Coliidae for two of the five fossil localities for this clade (Messel and Walton-on-the-Naze). Ecological models were significantly better at predicting fossil occurrences than random expectations based on binomial tests ($p < 0.05$), regardless of threshold or paleo-plate model choice, except for Leptosomidae (significant at $\alpha = 0.096$ for LTP threshold, and $\alpha = 0.078$ for MaxSSS threshold) and Todidae, for which models failed to predict fossil occurrences. Estimates of suitable habitat were more restricted when using the MaxSSS threshold (*versus* LTP threshold), resulting in fewer predicted occurrences for this threshold method (Table 1). The restricted geographic distributions predicted for Leptosomidae and Todidae in the Paleogene are likely a result of their especially narrow present-day distributions, which may complicate ecological modeling (40): Leptosomidae are found only in Madagascar, Mayotte, and the neighboring Comoro Islands, while Todidae are endemic to the Greater Antilles and small adjacent islands (41).

Novel environmental combinations can be encountered when projecting ecological models to different regions and/or time periods (42). In these instances, it is difficult to determine, using correlative approaches, whether these unique climatic conditions would be suitable for occupancy by species and higher clades. Although areas predicted as suitable in our

paleo-projections were unaffected by novel climate combinations, novel climates were estimated at low latitudes (from approx. ±23º latitude) from the Ypresian–Chattian. These novel combinations derived primarily from warmer minimum and maximum monthly temperatures estimated for the Paleogene than exist today. Therefore, whether tropical latitudes would have been suitable for these clades in deep time, especially given estimates of extreme Eocene warmth, remains an open question (43). Discoveries of Paleogene fossil birds from low-latitudes will be of major importance for clarifying the composition of tropical avian communities in deep time (12).

Most suitable area in the Ypresian was inferred at fairly high latitudes (~40–50º), with the bulk of suitable habitat shifting equator-ward in a stepwise manner towards the present (Fig 3). This pattern is evident across all examined clades, with the sharpest contractions of habitable distributions coinciding with the Eocene–Oligocene transition (44, 45), and the next sharpest occurring in the Neogene (Fig. 3 & Fig. S31). As a result, the latitudinal centroid of estimated suitable habitat for each clade moved equator-ward through time (Fig. 3 & Fig. S31).

Discussion

Models of suitable conditions for neornithine clades calibrated using modern-day distributional and climate data were able to accurately predict the distributions of these clades' fossil stem-group representatives through the Paleogene, a critical interval in avian evolutionary history during which many of the deepest neornithine phylogenetic divergences are inferred to have taken place (5, 6, 46). This predictive ability was not predicated on broad estimates of the paleo-distributions for studied clades, but rather on narrow bands of suitable habitat estimated at latitudes higher than those occupied by these clades today. Indeed, across our 10 focal clades, we

recovered an average difference of ~20º latitude between centroids of suitable habitat predicted for the Eocene (Ypresian) and those predicted for the present day (Fig. 3 and Fig. S31).

The importance of our results is twofold. First, our methods assumed that niche models conditioned on the modern geographic distributions of avian clades accurately encompassed the climatic tolerances of their early stem-group representatives. Although an important source of uncertainty, evidence supporting conservation of clade tolerances over evolutionary timescales has been reported in a variety of clades (47-56). It is striking that we were able to use present-day models of clade tolerances to accurately predict paleo-distributions for these clades' stem-group relatives under conditions estimated to have occurred up to ~56 million years ago, especially in light of the varied ecological habits and geographic distributions of the clades studied (Fig. 1 and 2). As such, our results provide first-order support for conservatism of the coarse-scale manifestations of species temperature and precipitation tolerances over geological timescales.

Second, we corroborate climate as a major long-term driver of crown neornithine biogeographic patterns (57, 58). Niche models calibrated on extant clade-level data and projected onto Ypresian–Chattian paleoclimatic reconstructions predicted shifts through time in the centroid of estimated habitable areas of more than 20° latitude for all examined clades. These analyses suggest that Cenozoic climatic change may have been predominantly responsible for driving dramatic shifts in the geographic distributions of these avian clades.

Both Cenozoic paleobiogeography (11, 12, 14, 19, 36, 59) and the timing of the extant neornithine radiation (4-7) cast doubt on Mesozoic Gondwanan vicariance as the mechanism underlying the extreme modern asymmetry of endemic higher-order neornithine diversity in the

Southern and Northern Hemispheres, raising questions about the origin of pervasive trans-Antarctic avian distributional patterns (2, 60).

A detailed stratigraphic analysis of the European fossil bird record suggests that the assembly of modern avian biogeographic distributions biased toward equatorial latitudes may be the product of two independent waves of geographic range contraction by avian clades throughout the Cenozoic (58). That study noted that a comparatively recent Miocene wave of European extinctions seems to have overwhelmingly affected representatives of clades that are now found in the modern Afrotropical zoogeographic zone (e.g., mousebirds, Coliiformes), or which currently exhibit pantropical distributions (e.g., parrots, Psittaciformes and trogons, Trogoniformes). In contrast, earlier Paleogene extinctions seem to have eliminated taxa whose crown-group representatives are now found in the neotropics, Madagascar, and Australasia (58). Mayr (12, 58) argued that extirpation of 'tropical' European taxa during the Paleogene cannot be attributed reliably to climatic cooling during this period (*contra* 61), since many 'tropical' taxa persisted into the cooler Oligocene and even into the early Neogene. However, the extirpation of 'tropical' neornithine taxa in the Paleogene of North America (e.g., 11) may be more reliably attributed to ecosystem changes related to cooling throughout the Eocene (58). Our inferred patterns of long-term contraction of habitable distributions throughout the Neogene (Fig. 3) are consistent with Miocene climatic cooling driving extirpations and equator-ward range contractions (58).

'Paratropical' forests indicative of well-watered, warmer, and more-equable climates, such as those persisting at lower latitudes today (62-64), were widespread across North America during the Eocene, and coincided with the presence of stem taxa whose crown group representatives are now restricted to lower latitudes. The distribution of these megathermal

climates (*sensu* 65) and associated forests in North America declined substantially toward the end of the Eocene, which had a profound effect on the diversity and composition of North American mammalian and squamate communities (66-70). If many taxa comprising the Paleogene North American avifauna were adapted to megathermal conditions, the extirpation of these taxa from North America may reflect the elimination of these warmer habitats at higher latitudes, resulting in a sharpening of the latitudinal biodiversity gradient (53, 71). Under a model of phylogenetic niche conservatism, habitat tracking may result in broad-scale range constriction, across multiple clades, in response to climate change (69). Indeed, investigations of early Eocene squamate faunas from North America suggest that taxa once common at mid-latitudes may have contributed substantially to populating lower-latitude biotas in the present day (69). The neornithine fossil record from North America during this interval appears to corroborate this pattern, emphasizing the critical relevance of paleontological data to our understanding of the historical biogeography of extant clades (57, 72).

Estimating the areas of origin of major extant bird clades has emerged as an especially controversial topic in contemporary bird systematics (36, 73), despite ever-improving historical biogeographic models (e.g., 74, 75) and large-scale avian molecular phylogenies (4-6, 76, 77). We suggest that a primary focus on inferring deep-time areas of origin for major bird clades, which may not be unambiguously discernible given our present knowledge of the avian fossil record (11, 69), overlooks a more achievable goal: discerning the mechanisms that have driven avian range evolution throughout the Cenozoic. This would result in a clearer picture of how and when major avian subclades are likely to have acquired their present-day distributions. We provide quantitative evidence that protracted environmental change throughout the Cenozoic has forced the long-term, equator-ward contraction of avian geographic distributions. Delineating

between competing biogeographic models whereby major extant clades presently restricted to the tropics originated at low latitudes, or simply became restricted to these areas over the course of the Cenozoic, will rely on renewed focus on Cenozoic fossil avifaunas from Gondwanan continents (12, 78, 79). However, such work has already recovered evidence of extant lineages with restricted distributions, such as Opisthocomiformes (represented today only by the Amazonian endemic *Opisthocomus hoazin*) occurring on additional Gondwanan and Laurasian continents throughout the Neogene (80, 81).

Although the early Cenozoic avian fossil record is rich (e.g., 12), important temporal and geographical gaps remain. Considering our evidence for apparent avian niche conservatism and habitat tracking over geological timescales, we suggest the application of ecological modeling tools may provide a first approximation of regions likely to have been inhabited by various bird groups through time, which may aid in guiding paleontological exploration.

Predicting the influence of human-induced climatic change on short- and long-term organismal distributions is an urgent goal in contemporary biology, and projections of major geographic range shifts in the face of Earth's current climatic trajectory are becoming ever more common (e.g., 82, 83, 84). As arguably the most vagile of the major groups of living vertebrates, birds may be more likely than others to undergo dramatic saltational shifts in their geographic distributions, evidenced by historical transoceanic colonization of new continents by extant bird species within historical memory (e.g., 85, 86). Marginalized across geographic timescales, the frequency of such stochastic dispersal events may explain the apparent habitat-tracking success of birds through the Cenozoic, provided that newly-colonized areas are suitable for long-term occupancy by the pioneering species. Although explicit predictions are beyond the scope of the present work, our conclusions would seem to suggest that climatic changes over the

coming decades and centuries may induce major distributional changes across the avian tree of life, as has been suggested recently for corals in the marine realm (84). The extremely rapid pace of anthropogenic climate change, however, may instead make it more likely that major groups with restricted distributions are driven to extinction *in situ*. Unraveling the relative likelihood of these outcomes will be an important goal of future work in avian biogeography and macroecology.

Methods

Full details of our methods are presented in the Supplementary Information, including details of clade selection and model caveats.

Ecological model inputs

Distributional data for each extant species within our focal clades were drawn from the Global Biodiversity Information Facility (www.gbif.org) (Fig. 1; Figs. S21-30). To characterize present-day climatic landscapes for ecological modeling, we used four environmental variables at 5' spatial resolution from the WorldClim bioclimatic data set (87): maximum temperature of warmest month, minimum temperature of coldest month, precipitation of the wettest month, and precipitation of the driest month. Estimates of past climates were simulated for four time periods: Ypresian (~56–47.8 Ma), Priabonian (~37.8–33.9 Ma), Rupelian (~33.9–28.1 Ma) and Chattian (~28.1–23.03 Ma). Data were derived from Paleogene simulations produced by two general circulation models (GCMs): FAMOUS (88) and HadCM3L (89, 90).

Ecological modeling

Clade tolerances were quantified using Maxent v.3.3.3k, a maximum entropy algorithm that estimates suitable environmental combinations for species under a null expectation that suitability is proportional to availability (39). We used present-day environmental conditions to constrain clade tolerances, and resulting models were then projected onto Eocene and Oligocene climatic conditions to estimate the geographic regions that would have been suitable for these clades from the Ypresian through the Chattian. Resulting ecological models produced estimates of suitable abiotic conditions for clades based on present-day climatic characterizations, without consideration of dispersal or biotic constraints.

Post-modeling analyses

We assessed the ability of paleo-projections of suitable habitat to correctly predict fossil occurrence localities. The correspondence between fossil sites and paleo-projections was analyzed as follows: fossil sites were transformed (paleo-rotated) so that they reflected their geographical position during the period in which they were deposited. Two paleo-plate models were used for transformations: Getech (see (91) and EarthByte via the PaleoGIS extension for ArcGIS (92)). Localities were accorded a buffer of 25 km using the 'gBuffer' function in the 'rgeos' package for *R* (93). Localities were buffered to account for uncertainty in both paleo-plate rotations and georeferencing, and to reflect the minimum likely area the fossil would have occupied when extant. These buffered localities were then intersected with the suitable area predicted for the time period corresponding to the age of the fossil site using a custom script written in *R*.

We assessed the probability of randomly predicting fossil occurrences for each clade in each time slice using binomial tests (94). Analyses were performed for each clade characterized

by more than one occurrence in a given time slice, using the following parameters: n = the number of successfully-predicted occurrences, K = the total number of occurrences, and p = the probability of successfully predicting an occurrence, defined by the percentage of predicted suitable terrestrial area globally.

Temporal shifts in the centroid of suitable habitat predicted for each clade were calculated using the 'gCentroid' function in the 'rgeos' package for *R* (93). The binary suitability maps were converted to polygons, and these polygons were used to find the 'center of mass' (also known as 'true centroid') of the areas presenting suitable conditions for each time slice; Northern and Southern Hemispheres were calculated separately (Fig. 3; Fig. S31).

Acknowledgments.

We thank Michelle Casey (Towson University, USA) for advice on paleo-plate rotation models. EES was supported by an EAR NSF Postdoctoral Fellowship and Leverhulme Grant #DGR01020. A. Farnsworth and D.J. Lunt were funded by the UK National Environmental Research Council (NE/K014757/1; NE/I005722/1; NE/I005714/1 and NE/P013805/1).

Author Contributions

E.S. and D.J.F. designed the study, collected the data, and wrote the manuscript. A.F., N.S., and D.L. contributed climate modeling data. E.S. and K.V.P. performed analyses. All authors read and commented on the manuscript.

Figure Legends.

Table 1. Correspondence of paleo-projections with penecontemporaneous fossils. Least training presence (LTP) and MaxSSS threshold methods are shown for the two paleo-plate rotational models (EarthByte and Getech Plc.). Predicted suitable area for each paleo-projection is shown as a percentage of terrestrial areas globally.

Fig. 1. Present-day occurrences for the 10 neornithine clades studied. Geographic ranges are circumtropical and predominantly restricted to vestiges of Gondwana (Africa, South America, and Australasia).

Fig. 2. Present-day occurrences (bottom panel) for Coliidae as derived from GBIF. Using these occurrences, models of abiotic tolerances for this clade were projected onto estimates of past climate conditions at the Ypresian (~56 Ma), the approximate time when fossil representatives of these groups were deposited. Note the accurate correspondence between fossil localities (shown on map) and model predictions. Maps are shown for both the least training presence (LTP; green) and MaxSSS (blue) threshold methods; pink and white occurrences represent Getech and EarthByte paleo-plate rotational models, respectively (see Methods for details). For other clades, see Figs. S21-30.

Fig. 3. Temporal shifts in the centroid of suitable habitat for each clade. Binary suitability maps were converted to polygons and used to find the ‘center of mass’ for areas presenting suitable conditions in each time slice; Northern (blue) and Southern (green) Hemispheres were calculated separately. Results are shown for the least training presence (LTP) threshold; see Fig. S31 in Supplementary Materials for MaxSSS threshold results.

Clade	Geological Stage	LTP threshold—% of correctly-predicted fossils			MaxSSS threshold—% of correctly-predicted fossils			# unique localities	Fossil localities
		EarthByte	Getech	% suitable area	EarthByte	Getech	% suitable area		
Anseranatidae	Ypresian	100%	100%	10.93	100%	100%	6.99	1	Walton-on-the-Naze
Cariamidae	Ypresian	100%	100%	19.50	100%	100%	11.08	1	Messel
Coliidae	Ypresian	100%	100%	19.00	100%	100%	13.50	4	Walton-on-the-Naze, Messel, Bridger & Willwood
	Priabonian	100%	100%	18.94	0%	0%	11.32	1	Florissant[*]
Leptosomidae	Ypresian	50%	50%	4.93	50%	50%	3.96	2	Green River, Walton-on-the-Naze[^]
Musophagidae	Ypresian	100%	100%	21.31	100%	100%	12.54	1	Green River
Nyctibiidae	Ypresian	100%	100%	8.47	100%	100%	7.59	1	Messel
Podargidae	Ypresian	100%	100%	23.61	100%	100%	15.34	2	Messel, Green River
Steatornithidae	Ypresian	100%	100%	10.87	100%	0%	9.16	1	Green River[#]
Todidae	Rupelian	0%	0%	3.95	0%	0%	3.75	2	Brule Formation, Wiesloch-Frauenweiler[$]
Trogonidae	Ypresian	100%	100%	21.86	100%	100%	13.69	2	Walton-on-the-Naze, Messel
	Rupelian	100%	100%	22.26	100%	0%	16.09	1	Lubéron[&]

[*]The unpredicted occurrence was within ~150 km of suitable area for both paleo-plate models

[^]The Green River locality is ~300 km away from suitable area

[#]The unpredicted occurrence is within ~150 km of suitable area

[$]Occurrences are over 300 km from suitable area for both paleo-plate and threshold models

[&]The unpredicted occurrence is within ~150 km of suitable area

Table 1

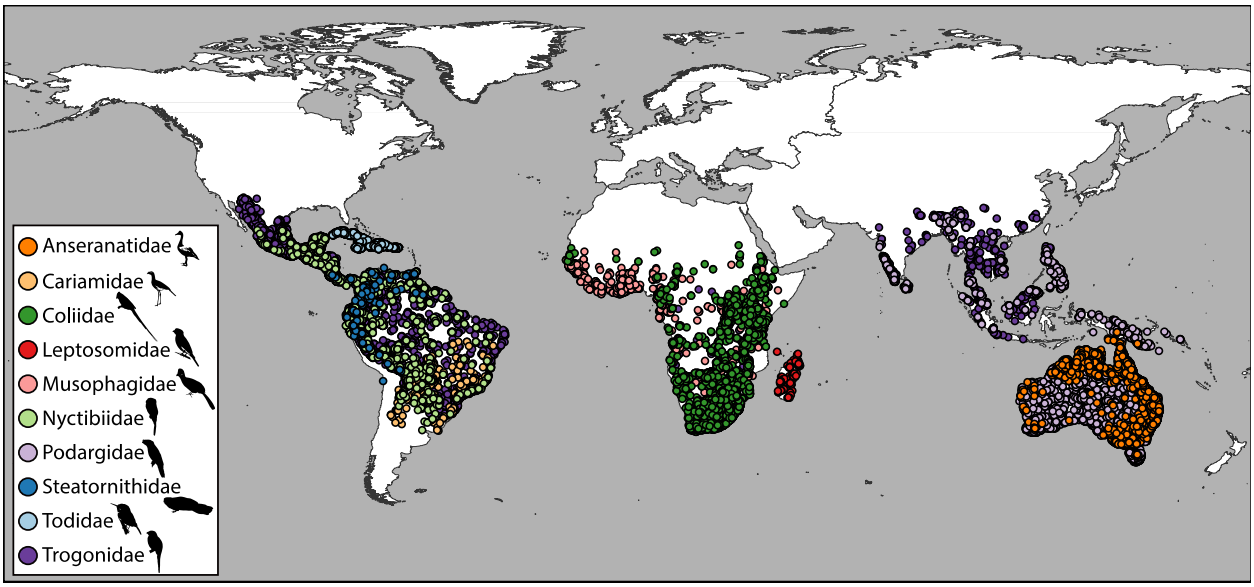

Fig. 1

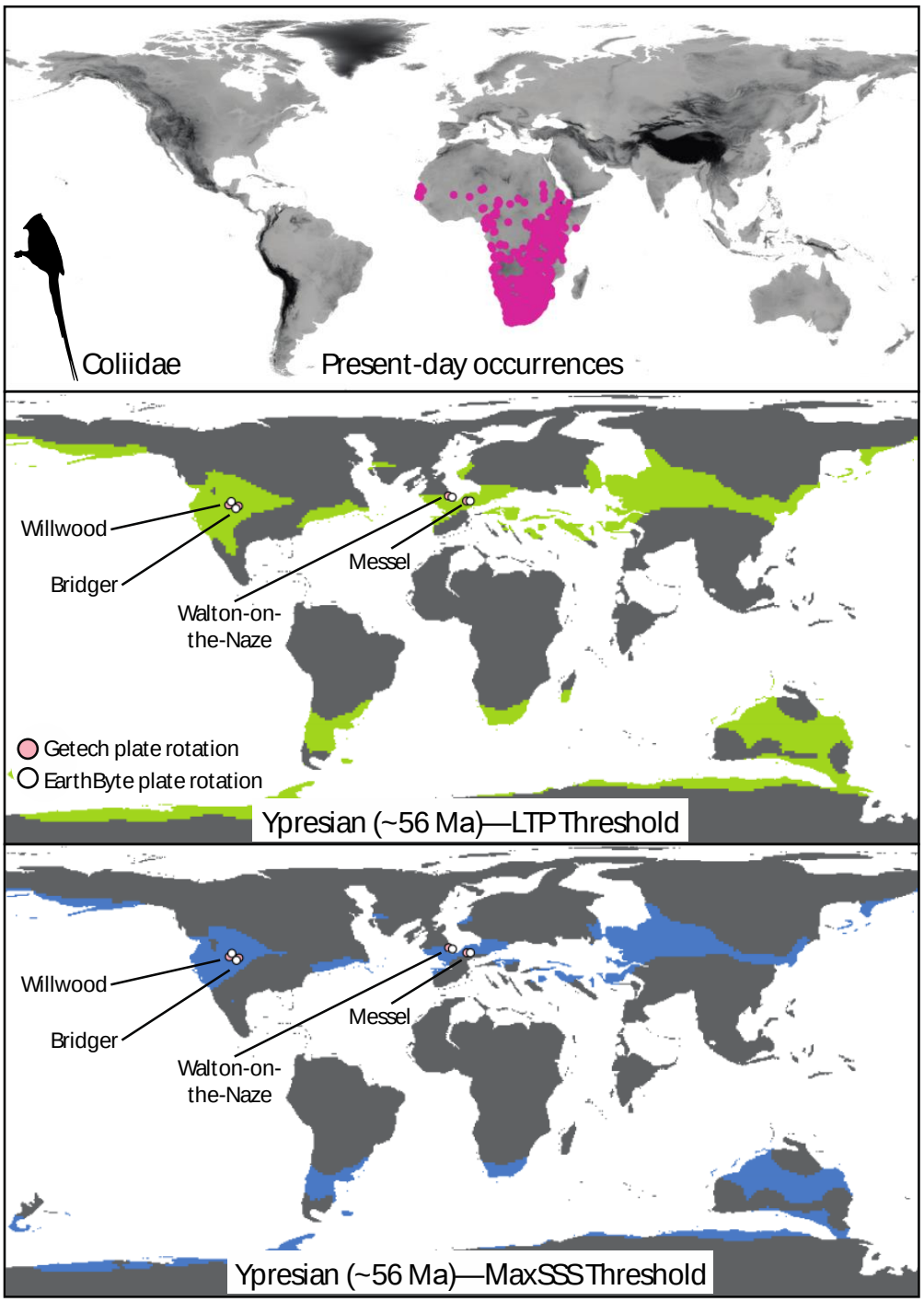
Coliidae
Present-day occurrences
Willwood
Bridger
Walton-on-
the-Naze
Messel
Getech plate rotation
EarthByte plate rotation
Ypresian (~56 Ma)—LTP Threshold
Willwood
Bridger
Walton-on-
the-Naze
Messel
Ypresian (~56 Ma)—MaxSSS Threshold

Fig. 2

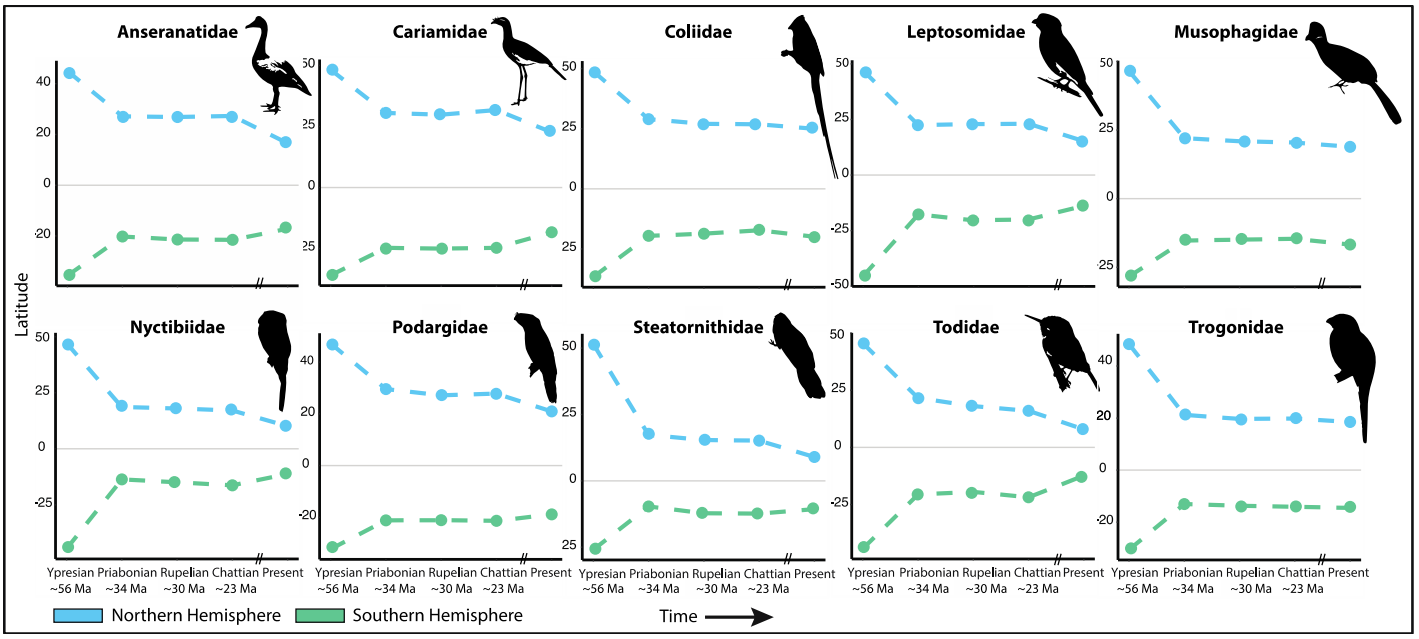
Anseranatidae
Cariamidae
Coliidae
Leptosomidae
Musophagidae
Nyctibiidae
Podargidae
Steatornithidae
Todidae
Trogonidae
Latitude
Ypresian ~56 Ma
Priabonian ~34 Ma
Rupelian ~30 Ma
Chattian ~23 Ma
Present
Northern Hemisphere
Southern Hemisphere
Time

Fig. 3

References

1. Gill F & Donsker D eds (2017) *IOC World Bird List v.7.3*).
2. Cracraft J (2001) Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society B: Biological Sciences* 268:459-469.
3. Ericson PGP*, et al.* (2006) Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* 2:543-547.
4. Jarvis ED*, et al.* (2014) Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346(6215):1320-1331.
5. Prum RO*, et al.* (2015) A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526(7574):569-573.
6. Claramunt S & Cracraft J (2015) A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advances* 1:e1501005.
7. Berv JS & Field DJ (2018) Genomic Signature of an Avian Lilliput Effect across the K-Pg Extinction. *Systematic Biology* 67(1):1-13.
8. Clyde WC, Ramezani J, Johnson KR, Bowring SA, & Jones MM (2016) Direct high-precision U–Pb geochronology of the end-Cretaceous extinction and calibration of Paleocene astronomical timescales. *Earth and Planetary Science Letters* 452:272-280.
9. Scher HD & Martin EE (2006) Timing and climatic consequences of the opening of drake passage. *Science* 312(5772):428-430.
10. Livermore R, Hillenbrand CD, Meredith M, & Eagles G (2007) Drake Passage and Cenozoic climate: An open and shut case? *GGG* 8(1):Q01005.
11. Field DJ & Hsiang AY (2018) A North American stem turaco, and the complex biogeographic history of modern birds. *BMC Evol Biol* 18:102.
12. Mayr G (2009) *Paleogene Fossil Birds* (Springer, Berlin) p 262.
13. Mourer-Chauviré C (1982) Les oiseaux fossiles des phosphorites du Quercy (Éocène supérieur a Oligocène supérieur): Implications paléobiogéographiques. *Geobios* 15, Supplement 1:413-426.
14. Olson SL (1989) Aspects of global avifaunal dynamics during the Cenozoic. *Acta XIX congressus internationalis ornithologici*, ed Ouellet H (University of Ottawa Press, Ottawa), Vol 2, pp 2023-2029.
15. Mayr G (2002) Avian Remains from the Middle Eocene of the Geiseltal (Sachsen-Anhalt, Germany). *Proceedings of the 5th symposium of the Society of Avian Paleontology and Evolution. Beijing, 1–4 June 2000*, eds Zhou Z & Zhang F (Science Press, Beijing), pp 77-96.
16. Mayr G (2000) New or previously unrecorded avian taxa from the Middle Eocene of Messel (Hessen, Germany). *Mitt Mus Naturkd Berl Geowiss Reihe* 3:207-219.
17. Peters DS (1995) *Idiornis tuberculata* n. spec., ein weiterer ungewöhnlicher Vogel aus der Grube Messel (Aves: Gruiformes: Cariamidae: Idiornithinae). *Acta Palaeornithologica*, ed Peters DS (Cour Forsch Inst Senckenberg, Frankfurt), Vol 181, pp 107-119.
18. Mourer-Chauviré C (1983) Les Gruiformes (Aves) des Phosphorites du Quercy (France). 1. Sous-ordre Cariamae (Cariamidae et Phorusrhacidae). *Palaeovertebrata* 13(4):83-143.

19. Mourer-Chauviré C (1999) Les relations entre les avifaunes du Tertiaire inférieur d'Europe et d'Amérique du Sud. *Bulletin de la Société Géologique de France* 170(1):85-90.
20. Mourer-Chauviré C (2006) The avifauna of the Eocene and Oligocene Phosphorites du Quercy (France): An updated list. *Strata* 13(13):135-149.
21. Ksepka DT & Clarke JA (2009) Affinities of *Palaeospiza bella* and the phylogeny and biogeography of mousebirds (Coliiformes). *The Auk* 126(2):245-259.
22. Mayr G & Peters D (1998) The mousebirds (Aves: Coliiformes) from the Middle Eocene of Grube Messel (Hessen, Germany). *Senckenbergiana lethaea* 78(1-2):179-197.
23. Mayr G (2002) A new species of *Plesiocathartes* (Aves:? Leptosomidae) from the middle Eocene of Messel, Germany. *PaleoBios* 22(1):10-20.
24. Olson SL (1999) The anseriform relationships of Anatalavis Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. *Smithsonian Contributions to Paleobiology* 89:231-243.
25. Olson SL (1987) An early Eocene oilbird from the Green River Formation of Wyoming (Caprimulgiformes: Steatornithidae). *Documents des Laboratoires de Géologie de Lyon* 99:57-69.
26. Mayr G (2005) The Palaeogene Old World potoo Paraprefica Mayr, 1999 (Aves, Nyctibiidae): its osteology and affinities to the New World Preficinae Olson, 1987. *Journal of Systematic Palaeontology* 3:359-370.
27. Nesbitt SJ, Ksepka DT, & Clarke JA (2011) Podargiform Affinities of the Enigmatic *Fluvioviridavis platyrhamphus* and the Early Diversification of Strisores ("Caprimulgiformes" + Apodiformes). *PLoS ONE* 6(11):e26350.
28. Mayr G (2001) Comments on the osteology of Masillapodargus longipes Mayr 1999 and Paraprefica major Mayr 1999, caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). *Neues Jahrbuch fur Geologie und Palaontologie - Monatshefte* (2):65-76.
29. Mourer-Chauviré C (1989) Les Caprimulgiformes et les Coraciiformes de l'Eocène et de l'Oligocène des Phosphorites du Quercy et description de deux genres nouveaux de Podargidae et Nyctibiidae. *Acta XIX Congressus Internationalis Ornithologici*:2047-2055.
30. Mayr G & Knopf C (2007) A tody (Alcediniformes, Todidae) from the early Oligocene of Germany. *The Auk* 124:1294-1304.
31. Mourer-Chauviré C (1985) Les Todidae (Aves, Coraciiformes) des Phosphorites du Quercy (France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B* 88:407-414.
32. Olson SL (1976) Oligocene fossils bearing on the origins of the Todidae and the Momotidae (Aves: Coraciiformes). *Smithsonian Contributions to Paleobiology* 27:111-119.
33. Mayr G (2001) A second skeleton of the early Oligocene trogon Primotrogon wintersteini Mayr 1999 (Aves: Trogoniformes: Trogonidae) in an unusual state of preservation. *Senckenbergiana lethaea* 81(2):335-338.
34. Mayr G (1998) An archaeotrogon (Aves: Archaeotrogonidae) from the Middle Eocene of the Grube Messel (Hessen, Germany)? *Journal fur Ornithologie* 139(2):121-129.

35. Mourer-Chauviré C (1980) The Archaeotrogonidae of the Eocene and Oligocene Phosphorites du Quercy (France). *Contributions to Science of the Natural History Museum Los Angeles County* 330(330):17-31.
36. Mayr G (2017) Avian higher level biogeography: Southern Hemispheric origins or Southern Hemispheric relicts? *J Biogeogr* 44:956-958.
37. Waterson AM*, et al.* (2016) Modelling the climatic niche of turtles: a deep-time perspective. *Proceedings of the Royal Society B: Biological Sciences* 283(1839):20161408.
38. Chiarenza AA*, et al.* (2019) Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature Communications* 10(1):1091.
39. Phillips SJ, Anderson RP, & Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231-259.
40. Saupe E*, et al.* (2012) Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. *Ecological Modeling* 237:11-22.
41. Del Hoyo J, Elliot A, & Sargatal J (1992) Handbook of the Birds of the World. (Lynx Editions, Barcelona).
42. Owens HL*, et al.* (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Journal of Ecological Modelling* 263:10-18.
43. Inglis GN*, et al.* (2017) Mid-latitude continental temperatures through the early Eocene in western Europe. *Earth and Planetary Science Letters* 460:86-96.
44. Stehlin HG (1909) Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bull Soc Geol Fr* 19:488-520.
45. Meng J & McKenna MCJN (1998) Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature* 394(6691):364.
46. Jarvis ED*, et al.* (2014) Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346:1320-1331.
47. Strubbe D, Beauchard O, & Matthysen E (2015) Niche conservatism among non-native vertebrates in Europe and North America. *Ecography* 38(3):321-329.
48. Feldman A, Sabath N, Pyron RA, Mayrose I, & Meiri S (2015) Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography*:n/a-n/a.
49. Cooper N, Freckleton RP, & Jetz W (2011) Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B* 278(1716):2384-2391.
50. Peterson A, Soberón J, & Sánchez-Cordero VJS (1999) Conservatism of ecological niches in evolutionary time. 285(5431):1265-1267.
51. Saupe E*, et al.* (2014) Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. *Proceedings of the Royal Society B: Biological Sciences* 281(1795):20141995.
52. Prinzing A, Durka W, Klotz S, & Brandl R (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B. Biol. Sci.* 268(1483):2383-2389.
53. Hawkins BA, Diniz-Filho JAF, Jaramillo CA, & Soeller SA (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J Biogeogr* 33(5):770-780.

54. Crisp MD, *et al.* (2009) Phylogenetic biome conservatism on a global scale. *Nature* 458:754-756.
55. Rodrigues JFM, Villalobos F, Iverson JB, & Diniz-Filho JAF (2018) Climatic niche evolution in turtles is characterized by phylogenetic conservatism for both aquatic and terrestrial species. *J Evol Biol* 32:66-75.
56. Wiens John J, Graham Catherine H, Moen Daniel S, Smith Sarah A, & Reeder Tod W (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist* 168(5):579-596.
57. Blondel J & Mourer-Chauviré C (1998) Evolution and history of the western Palaearctic avifauna. *Trends in Ecology and Evolution* 13(12):488-492.
58. Mayr G (2011) Two-phase extinction of "Southern Hemispheric" birds in the Cenozoic of Europe and the origin of the Neotropic avifauna. *Palaeobiodiversity and Palaeoenvironments* 91:325-333.
59. James HF (2005) Paleogene fossils and the radiation of modern birds. *The Auk* 122(4):1049-1054.
60. Cracraft J (1973) Continental drift, paleoclimatology, and the evolution and biogeography of birds. *Journal of Zoology* 169(4):455-543.
61. Lindow BEK & Dyke GJ (2006) Bird evolution in the Eocene: climate change in Europe and a Danish fossil fauna. *Biological Reviews* 81(04):483-499.
62. Grande L (2013) *The Lost World of Fossil Lake: Snapshots from Deep Time* (University of Chicago Press, Chicago, Illinois).
63. MacGinitie HD (1969) The Eocene Green flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Science* 83:1-149.
64. Grande L (1994) The Tertiary Green River Lake Complex, with comments on paleoenvironments and historical biogeography. *Symposium volume on Early Tertiary paleontology and environments in Wyoming. Contributions to Geology* 30:3-14.
65. van Steenis CGGJ (1962) The land-bridge theory in botany with particular reference to tropical plants. *Blumea-Biodiversity, Evolution and Biogeography of Plants* 11(2):235-372.
66. Webb SD (1977) A history of savanna vertebrates in the New World. Part I: North America and the Great Interchange. *Annu. Rev. Ecol. Syst.* 8:355-380.
67. Janis CM (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology & Evolution* 24:467-500.
68. Cox CB (2000) Plate tectonics, seaways and climate in the historical biogeography of mammals. *Mem Inst Oswaldo Cruz* 95:509-516.
69. Smith KT (2009) A new lizard assemblage from the earliest Eocene (Zone Wa0) of the Bighorn Basin, Wyoming, USA: Biogeography during the warmest interval of the Cenozoic. *Journal of Systematic Palaeontology* 7(3):299-358.
70. Gauthier JA (1982) Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, Southeast Wyoming, and a revision of the Anguioidea. *Rocky Mountain Geology* 21(1):7-54.
71. Mannion PD, Upchurch P, Benson RBJ, & Goswami A (2014) The latitudinal biodiversity gradient through deep time. *Trends Ecol Evol* 29:42-50.

72. Ksepka DT & Thomas DB (2011) Multiple cenozoic invasions of Africa by penguins (Aves, Sphenisciformes). *Proceedings of the Royal Society of London B: Biological Sciences* 279:1027-1032.
73. Cracraft J & Claramunt S (2017) Conceptual and analytical worldviews shape differences about global avian biogeography. *J Biogeogr* 44:958-960.
74. Yu Y, Harris AJ, Blair C, & He X (2015) RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87:46-49.
75. Landis MJ, Matzke NJ, Moore BR, & Huelsenbeck JP (2013) Bayesian analysis of biogeography when the number of areas is large. *Systematic biology* 62(6):789-804.
76. Jetz W, Thomas GH, Joy JB, Hartmann K, & Mooers AO (2012) The global diversity of birds in space and time. *Nature* 491:444-448.
77. Oliveros CH*, et al.* (2019) Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences* 116(16):7916-7925.
78. Field DJ (2017) Preliminary paleoecological insights from the Pliocene avifauna of Kanapoi, Kenya: Implications for the ecology of *Australopithecus anamensis*. *Journal of Human Evolution*.
79. Tambussi CD & Degrange FJ (2013) *South American and Antarctic Continental Cenozoic Birds: Paleobiogeographic Affinities and Disparities* (Springer, La Plata, Argentina).
80. Mayr G & De Pietri VL (2014) Earliest and first Northern Hemisphere hoatzin fossils substantiate Old World origin of a "Neotropic endemic". *Naturwissenschaften*.
81. Mayr G, Alvarenga H, & Mourer-Chauviré C (2011) Out of Africa: Fossils shed light on the origin of the hoatzin, an iconic Neotropic bird. *Naturwissenschaften* 98(11):961-966.
82. Bonebrake TC*, et al.* (2018) Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews* 93(1):284-305.
83. Pecl GT*, et al.* (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355(6332):eaai9214.
84. Jones LA*, et al.* (2019) Coupling of palaeontological and neontological reef coral data improves forecasts of biodiversity responses under global climatic change. *Royal Society Open Science* 6(4):182111.
85. Crosby GT (1972) Spread of the cattle egret in the Western Hemisphere. *Bird-Banding* 43(3):205-212.
86. Oswald JA*, et al.* (2019) Evolutionary dynamics of hybridization and introgression following the recent colonization of Glossy Ibis (Aves: Plegadis falcinellus) into the New World. *Molecular Ecology*.
87. Hijmans RJ, Cameron SE, Parra JL, Jones PG, & Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *IJCli* 25:1965-1978.
88. Sagoo N, Valdes P, Flecker R, & Gregoire LJ (2013) The Early Eocene equable climate problem: can perturbations of climate model parameters identify possible solutions? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 371(2001):20130123.

89. Kennedy AT, Farnsworth A, Lunt DJ, Lear CH, & Markwick PJ (2015) Atmospheric and oceanic impacts of Antarctic glaciation across the Eocene–Oligocene transition. *Philosophical Transactions of the Royal Society, A* 373:20140419.
90. Lunt DJ*, et al.* (2016) Palaeogeographic controls on climate and proxy interpretation. *CliPa* 12:1181-1198.
91. Lunt DJ*, et al.* (2016) Palaeogeographic controls on climate and proxy interpretation. *Climates of the Past* 12:1181-1198.
92. Seton M*, et al.* (2012) Global continental and ocean basin reconstructions since 200Ma. *Earth-Science Reviews* 113(3):212-270.
93. Bivand R & Rundel C (2016) rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-19.).
94. Anderson RP, Gómez-Laverde M, & Peterson AT (2002) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Glob Ecol Biogeogr* 11(2):131-141.